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Both, C; Visser, M E

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# The effect of climate change on the correlation between avian life-history traits

CHRISTIAAN BOTH[1] and MARCEL E. VISSER
*Netherlands Institute of Ecology (NIOO-KNAW), PO Box 40, 6666 ZG Heteren, The Netherlands*

**Abstract**

**The ultimate reason why birds should advance their phenology in response to climate change is to match the shifting phenology of underlying levels of the food chain. In a seasonal environment, the timing of food abundance is one of the crucial factors to which birds should adapt their timing of reproduction. They can do this by shifting egg-laying date (LD), and also by changing other life-history characters that affect the period between laying of the eggs and hatching of the chicks. In a long-term study of the migratory Pied Flycatcher, we show that the peak of abundance of nestling food (caterpillars) has advanced during the last two decades, and that the birds advanced their LD. LD strongly correlates with the timing of the caterpillar peak, but in years with an early food peak the birds laid their eggs late relative to this food peak. In such years, the birds advance their hatching date by incubating earlier in the clutch and reducing the interval between laying the last egg to hatching of the first egg, thereby partly compensating for their relative late LD. Paradoxically, they also laid larger clutches in the years with an early food peak, and thereby took more time to lay (i.e. one egg per day). Clutch size therefore declined more strongly with LD in years with an early food peak. This stronger response is adaptive because the fitness of an egg declined more strongly with date in early than in late years. Clearly, avian life-history traits are correlated and Pied Flycatchers apparently optimize over the whole complex of the traits including LD, clutch size and the onset of incubation. Climate change will lead to changing selection pressures on this complex of traits and presumably the way they are correlated.**

*Keywords:* climate change, clutch size, *Ficedula hypoleuca*, food availability, laying date

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## Introduction

There is a growing body of evidence which shows that climate change affects ecosystems, and especially the phenology of a wide array of organisms (Forchhammer *et al*., 1998; Post *et al*., 2001; Stenseth *et al*., 2002; Parmesan & Yohe, 2003). The ultimate consequences of the timing of reproduction depend to a large extent on the phenology of organisms at other trophic levels (Visser *et al*., 2004). A full understanding of how climate change impacts on organisms therefore requires studies that take this ecological context into account. One of the few examples addressing climate change in such a multitrophic perspective is the simplified food chain of oak, caterpillars and great tits in European woodlands (Perrins & McCleery, 1989; Visser *et al*., 1998; Buse *et al*., 1999; Visser & Holleman, 2001). In order to reproduce successfully, great tits should have their young in the nest when the caterpillars are most abundant (Perrins, 1965, 1970; van Balen, 1973; van Noordwijk *et al*., 1995), and caterpillars can only grow successfully if they hatch at the time the oak leaves are budding (van Dongen *et al*., 1997; Visser & Holleman, 2001). All components of this food chain are at least to some extent affected by temperature. Tit-laying dates (LD) are correlated with the caterpillar peak (Lack, 1966; Perrins & McCleery, 1989), but their responses to temperature differ, leading to a mismatch between the different components when temperature rises (Visser *et al*., 1998, 2004; Visser & Holleman, 2001).

As climate change has led to an advancement of the main food sources, individuals are expected to breed earlier (Crick *et al*., 1997; Winkel & Hudde, 1997;

Correspondence: Christiaan Both, e-mail: c.both@biol.rug.nl
[1]Present address: Animal Ecology Group, Center of Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands.

McCleery & Perrins, 1998; Crick & Sparks, 1999). The earlier breeding date is likely to affect other life-history decisions as well, because life-history traits within an organism are often correlated (Lack, 1966; Winkler *et al*., 2002). Climate change is therefore not expected to affect only the timing of reproduction, but rather the entire annual cycle (Coppack & Both, 2002). It is therefore important to establish how flexible the correlations are between life-history traits, because inflexible correlations will greatly constrain the response of a species to their changing environment. This will be particularly the case if there is a strong genetic correlation between life-history traits, as selection on one trait will have a direct response on the correlated trait, which may constrain adaptive responses to changing circumstances if genetic correlations are negative (Sheldon *et al*., 2003). Life-history traits may be correlated in an absolute way, as with genetically correlated traits, or in a more flexible way involving individuals adjusting their trait combination to the current environment, with such plasticity permitting a more adequate response to changing environments.

One of the life-history variables that changes simultaneously with LD is clutch size (Lack, 1966; Klomp, 1970; Daan *et al*., 1988; Winkler *et al*., 2002). von Haartman (1982) suggested that bird species differ in their clutch size response to LD, with Pied Flycatchers having a rather fixed response of their clutch size to calendar date, while Starlings adjust their clutch size to the breeding date relative to the timing of ecological circumstances. This is interesting, because Pied Flycatchers have advanced their LD during the last two decades (Winkel & Hudde, 1997; Slater, 1999; Both & Visser, 2001; Sanz, 2003; Both *et al*., 2004). As expected by von Haartmann's observations, this advancement was accompanied by an increase in clutch size (Winkel & Hudde, 1997; Both *et al*., 2004). However, the advancement of LD in this species has not been strong enough to match the advancement of spring (Both & Visser, 2001; Coppack & Both, 2002). The paradox, therefore, is that one would not expect these birds to lay more eggs, because this necessarily delays the hatching of the clutch (as they lay one egg per day), and thus results in an even greater mistiming of reproduction. In this paper we investigate how LD, clutch size and incubation time have changed over the years and how they are affected by the timing of the Pied Flycatchers' main prey, caterpillars (Sanz, 1998). Caterpillars are commonly fed to early broods and their importance declines over the season (von Haartman, 1954), matching the seasonal decline in fitness (Lack, 1966; Bauchau & Seinen, 1997; Siikamäki, 1998; Drent *et al*., 2003). Therefore, synchronizing hatching with the caterpillar peak date is likely to be important. We aim to explain how the correlation between the life-history traits, clutch size and LD might be affected by changing selection pressures because of climate change.

## Methods

Our long-term population study was carried out in the Hoge Veluwe area (central Netherlands) where approximately 400 nest boxes were provided from 1955 onwards. This area is a mixed forest, with Pedunculate Oak *Quercus robur,* Red Oak *Q. rubra,* Birch *Betula pubescens*, Pine *Pinus sylvestris* and Japanese Larch *Larix japonicus* as predominant tree species. Data were used from 1980 to 2004, because climate change in this period was more apparent than during the first 25 years of the study (IPCC, 2001). In addition, our population was growing rapidly during those initial years (Saether *et al*., 2002) and possible density-dependent effects are excluded by using the later period involving more stable population numbers. Nest boxes were visited once a week from the beginning of April to the beginning of July, and often daily from 2 days before the eggs were expected to hatch until hatching. LD is the day on which the first egg in the clutch was laid, which we determined by back counting and assuming that one egg was laid every day. In years nests were checked more intensively during laying (i.e. only 2 or 3 day intervals allowing checks both after the first egg and before the last egg were laid in that clutch), we found that for the 564 nest days in which we expected an egg to be laid, in only 1.2% of the cases no egg was laid. Thus, in 98.8% of days during laying one egg is laid every day. Clutch size is the number of eggs in a nest when the clutch was considered complete, i.e. the eggs were seen at least once during incubation or at least one of the eggs hatched. For the nests that were not visited daily close to hatching, hatching date was estimated from the development of the chicks. If observers were uncertain about the hatching time, the nest was not included in the analysis (total number of nests with a known hatching date: 1737). The laying–hatching (LH) interval was calculated as the number of days between the laying of the last egg and the hatching of the first egg in the nest. Nests in which experimental manipulations were carried out were excluded from the analyses, and the year 1995 is excluded altogether as about 90% of the nests were manipulated in this year (Bauchau & Seinen, 1997). Arithmetic means for each year for all nests in the population are used in the analyses.

In order to investigate whether the population responses are caused by phenotypic plasticity rather than a response to selection, we investigated whether individual females that bred twice in the population changed their clutch size vs. LD relationship in response to

changing environmental circumstances. For this analysis we selected the first and second breeding year of individually ringed females, and performed a mixed model with the identity of each female as a random factor in the analysis, and investigated whether the effect of LD on clutch size depended on the date of the caterpillar peak as well. We included a factor in the analysis to distinguish between first and second year, because females normally lay later and smaller clutches in their first year (Lundberg & Alatalo, 1992).

Temperature data used were the annual arithmetic mean of the daily mean between 16 April and 15 May, as recorded in The Bilt (about 50 km from the study area) by the Dutch Meteorological Service (KNMI). This time period roughly matches the period between the arrival of the first birds in the area in spring and the mean LD for at least the early years of the study. As a more biologically relevant measure of timing of the ecosystem, we used the time of the caterpillar peak during each year, as measured in the area using frass collectors (Tinbergen, 1960; Visser *et al.*, 1998). Frass collectors were emptied about once every 4–5 days, and caterpillar biomass was calculated from frass mass taking temperature-dependent metabolism into account (Tinbergen & Dietz, 1994). Peak date was the day with the highest calculated caterpillar biomass. This measure has been collected since 1985, and sample sizes are consequently slightly smaller for analyses including the caterpillar peak. All the statistics were performed on mean values per year, and tested using Pearson's correlations with two-tailed *P*-values.

In this paper we focus on the effect of LD on clutch size, and how the correlation between these life-history traits differs between years. The between-year variation in how clutch size was affected by LD was investigated by calculating the slope of the linear and quadratic component of a regression for each year. These slopes were then used to investigate whether the effect of LD on clutch size has changed over time and in relation to the caterpillar peak date.

To quantify changing selection pressures on the clutch size vs. LD relationship because of climate change, we calculated the fitness of fledglings depending on hatching date. For this, we determined the survival rates of an egg until breeding as adult by ringing all nestlings and retrapping them as breeding individuals in the same area. Egg to breeding survival was analysed with a logistic regression on all nests (dependent variable the number of recruits over the number of eggs), with year as factor and hatching date and its squared term and all interactions as independent variables. Trends over the years were examined in two ways: firstly, the annual slope of the interaction between year and hatching date was correlated with year as a continuous variable, and secondly, we analysed recruitment rate with year as a factor and hatching date as a main effect, and the interaction between the continuous variable of year and hatching date to examine whether the date effect changed over the years.

## Results

LD advanced 8 days in the period 1980–2004 ($r = -0.79$, $n = 24$, $P < 0.001$, Fig. 1a), and was negatively correlated with spring temperature ($r = -0.77$, $n = 24$, $P < 0.001$). At the same time clutch size increased significantly ($r = 0.79$, $n = 24$, $P < 0.001$, Fig. 1b), as would be predicted from the strong LD effect on clutch size, both between years on annual mean values ($r = -0.74$, $n = 24$, $P < 0.001$) and also within years (Both, 2000). The LH interval (the number of days between the laying of the last egg and the hatching of the first egg) declined throughout the years ($r = -0.53$, $n = 24$, $P = 0.008$, Fig. 1c), and was negatively correlated with temperature ($r = -0.48$, $n = 24$, $P = 0.020$). The interval between the laying of the first egg and hatching did not change over time ($r = -0.11$, $n = 24$, $P = 0.590$, Fig. 1d), and was unrelated to temperature ($r = -0.26$, $n = 24$, $P = 0.220$). So, despite the fact that the birds laid more eggs, birds did not increase the time between start of laying and

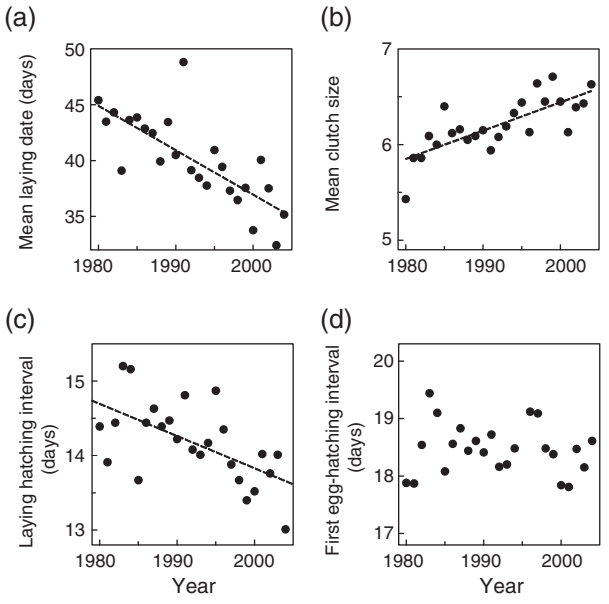


**Fig. 1** Annual reproductive parameters of Pied Flycatchers during the years 1980–2004 in a Dutch population involving (a) laying date in days since 31 March; (b) clutch size; (c) the interval between the laying of the last egg and hatching of the first egg; and (d) the interval between start of egg laying and hatching of the first egg.

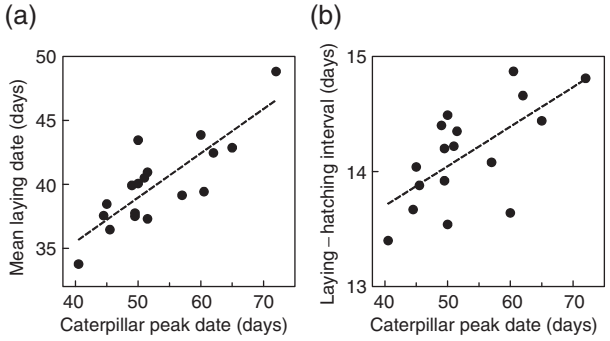


**Fig. 2** Annual reproductive parameters of Pied Flycatchers as a function of the date of the caterpillar peak (in days since 31 March) during the years 1985–2004 in a Dutch population involving (a) laying date in days since 31 March and (b) the interval between laying of the last egg and hatching of the first egg.

hatching, because at the same time they decreased the interval between the last egg and hatching. With each additional egg laid, this interval declined by 0.72 days.

LD and the LH were both correlated with the date of the caterpillar peak (LD: $r = 0.82$, $n = 19$, $P < 0.001$; LH: $r = 0.68$, $n = 19$, $P = 0.001$, Fig. 2). The interval between the start of laying and hatching was not significantly correlated with this measure of timing, although it approached significance ($r = 0.43$, $n = 19$, $P = 0.07$), suggesting that birds do speed up in years with an early food peak despite the increase in clutch size. Note that the flycatchers start laying on average well before the food peak (Fig. 2a), but that in early years the interval between laying and the caterpillar peak is only about 6 days, whereas in late years this interval can be as long as 22 days (slope of the regression of LD to caterpillar peak: + 0.39 (0.07), which is significantly different from 1: $t_{17} = -9.10$, $P < 0.001$; for hatching date the slope is + 0.41 (0.06), which is also different from 1: $t_{17} = -9.11$, $P < 0.001$). Thus, the response in LD to the shift in caterpillar peak appears incomplete. As a consequence, the mean hatching date in early years is about 10 days later than the caterpillar peak, but in late years chicks hatch on average 4 days before the caterpillar peak.

Although the increase in clutch size through time can be interpreted as the inevitable consequence of an environmentally insensitive reaction of clutch size to LD, this is not the case. The relationship between clutch size and LD differed between years (ANCOVA: year × LD: $F_{22,1849} = 4.27$, $P < 0.001$; LD squared: $F_{1,1849} = 31.71$, $P < 0.001$). The slope here was strongly correlated with the caterpillar peak date: in early years clutch size declined more strongly with LD than in late years (Fig. 3).

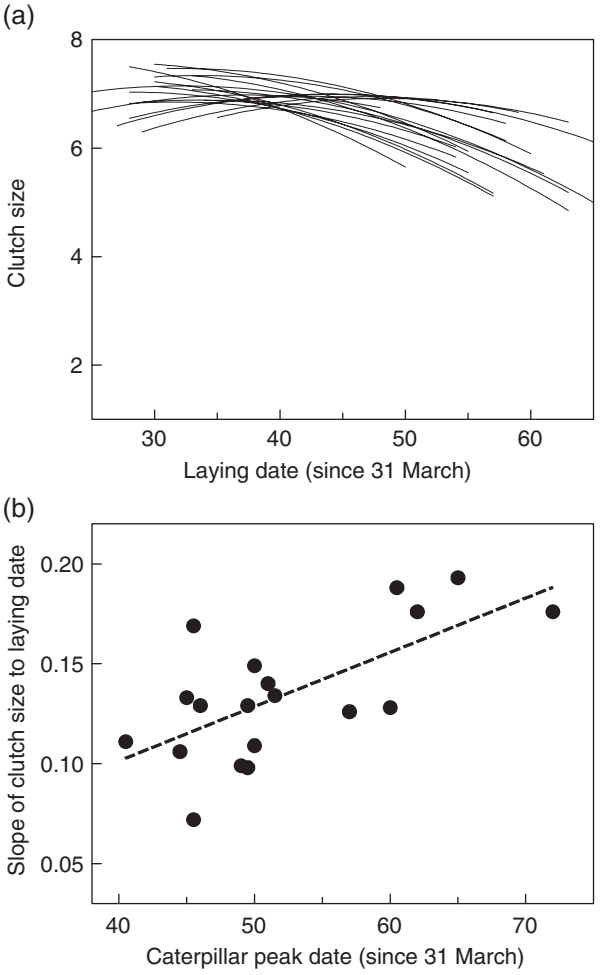


**Fig. 3** The strength of the relationship between clutch size and laying date (LD) in Pied Flycatchers as it relates to variation in the date of the caterpillar peak. Results are shown as (a) regression lines of clutch size against LD for each of the 19 years (1985–2004, excl. 1995) and (b) the annual slopes of the effect of LD on clutch size (as in (a)) from ANOVA in which LD squared was also included. This LD squared term did not differ among years, and its value was negative. The positive slopes in (b) do not therefore mean that clutch size increased with LD, and the lower the value, the steeper the date effect ($r = 0.67$, $n = 19$, $P = 0.001$).

Individual females that bred twice in the area adjusted their LD in response to the date of the caterpillar peak (mixed model with individual as random effect, age: $F_{1,258} = 6.16$, $P = 0.014$; caterpillar peak: $F_{1,258} = 124.75$, $P < 0.001$), and this within individual response ( + 0.37 (SE 0.033)) is very similar to the average population-level response ( + 0.35 (SE 0.061)). Females also adjusted clutch size to LD, laying larger clutches when they advanced their LD. Again, the strength of this relationship depended upon the date of the caterpillar peak: in years with an early caterpillar peak the response of clutch size to LD was stronger than

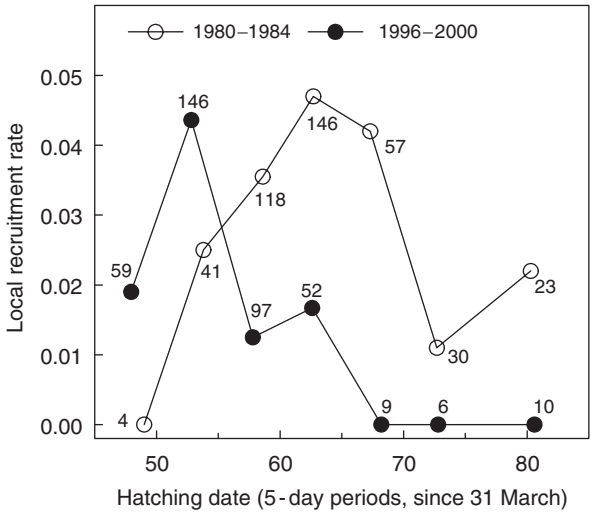


**Fig. 4** Changing fitness consequences of hatching date across years. For ease of presentation, the average probability that an egg results in a local recruit is calculated for 5 days blocks at a time (i.e. the last period is longer, and includes all nests hatching later than 15 June). Only two time periods of 5 years each are shown to demonstrate the finding that the fitness landscape changed over the years (statistical analysis was obviously performed using all years, see text). Recruitment probability was related to both hatching date and its squared term, and the slope of the regression changed over the years. The figures indicated are the number of nests upon which each data point is based.

in years with a late caterpillar peak (mixed model with individual as random effect, age: $F_{2,290} = 43.2$, $P = 0.001$; LD × caterpillar peak: $F_{1,290} = 4.55$, $P = 0.03$). At the individual level, for each day the caterpillar peak was delayed, the slope of LD on clutch size changed by 0.0012 (eggs/day) and this effect was almost identical to that at the population level (0.0011). The quantitatively similar effects of the caterpillar peak on the clutch size vs. LD relationship, found both at the population and the individual level, strongly suggest that it is individual plasticity that causes the greater declines in clutch size over the season in years with an earlier food peak.

Understanding why birds adapt their clutch size and incubation time to the changing phenology of their prey requires knowledge on how the fitness of an egg depends upon its hatching date relative to the timing of the food peak. Over the years, a shift occurred in the relationship between hatching date and recruitment rates. In the early 1980 the recruitment rate first increased and later decreased with hatching date, while in the later 1990 there was a general decline in recruitment rate with hatching date (Fig. 4). Recruitment was related to both hatching date and its squared term, and the slope of the regression changed over the years (logistic regression: year $\chi^2(18) = 42.65$, $P = 0.001$; hatching date$^2$: $\chi^2(1) = 3.75$, $P = 0.05$; year × hatching date: $\chi^2(1) = 10.50$, $P = 0.001$; see Fig. 4 for a graphical representation of date-related recruitment in the early and later period of the study). In an alternative analysis, we first determined the year-specific slopes of hatching date on recruitment rate (from a logistic regression with the interaction year × hatching date, including the squared term for hatching date), and correlated these slopes with year. This also showed that over the years of this study the negative effect of hatching date has increased (correlation $r = -0.77$, $n = 20$, $P = 0.0001$).

The change in the fitness consequences of LD over the years could, again, be caused by the advancement of the caterpillar peak. This is because, in years with an early food peak, the recruitment probability declined to a greater extent with hatching date than it did in years with a late caterpillar peak (correlation between the year-specific slope of hatching date on recruitment rate (from logistic regression) and caterpillar peak: $r = 0.52$, $n = 15$, $P = 0.05$). Thus, in years when the caterpillar peak was early, it proved important to be born early, because the likelihood of being recruited into the breeding population declined most strongly with hatching date in these years.

## Discussion

Pied Flycatchers breed earlier in warmer years, produce more eggs and reduce the interval between laying and hatching. The increase in ambient temperature during the 25 years of this study resulted in a strong effect on LD, clutch size and the LH interval over the years. However, despite the fact that the birds advanced their hatching by about 8 days, the response was not strong enough, as indicated by increasing selection for early breeding during this period (Both & Visser, 2001). We show here that birds partly compensate their insufficient LD response to climate change by reducing the interval between the laying of the last egg and hatching. This has also been observed in great tits: in one population with an inappropriate response to the timing of the food peak, birds reduced their LH interval (Visser *et al*., 1998), whereas in a population that may have responded too strongly, the birds increased their LH interval over the years (Cresswell & McCleery, 2003).

The observed increase in clutch size with an advancing LD seems to be consistent with von Haartmann's (1982) suggestion that clutch size of Pied Flycatchers is determined by calendar date, rather than by the date relative to some ecological factor, such as food. However, this is not the case. In years with an early food peak, clutch size declined more strongly with LD than in years with a late food peak. This is in contrast to the declines in clutch size with LD in warm and cold years observed by von Haartmann. Warm years were not only

characterized by an early food peak, but also by a shorter food peak. This is because insect growth and development are strongly temperature related, and caterpillars grow and pupate more rapidly in warm years, after which they are no longer available as food for the flycatchers (Buse *et al*., 1999). In addition, the number of caterpillars fed to the young declined strongly with date in our population (personal observation see also von Haartman, 1954). The greater decline of clutch size with LD in warm years is thus likely to be a response to a more rapid decline in food availability, and the relatively late LD as compared with the date of the food peak. This decline in clutch size is not a result of birds later in the season being of lower quality, because experimental delays showed that clutch size in individual females declined throughout the season (Bauchau & Seinen, 1997), as did fitness (Wiggins *et al*., 1994; Siikamäki, 1998). The steeper decline in clutch size in years with an early food peak was because late birds in those years laid smaller clutches, rather than the early birds laying larger clutches. The average clutch size in years with an early food peak is thus larger because more birds lay early, which more than counteracts the steeper decline in clutch size with the progress of the season.

Clutch size and LD are negatively genetically correlated in the closely related Collared Flycatcher *Ficedula albicollis* (Sheldon *et al*., 2003). This negative genetic correlation may constrain an adequate evolutionary response to global warming, because selection for early laying will also result in larger clutches, which may not be adaptive. This may, therefore, explain why we found both an advance of LD and an increase in clutch size with date. However, the advance in laying was mainly a phenotypic response of individual females adjusting their lay date to temperature (Przybylo *et al*., 2000; Both & Visser, 2001; Both *et al*., 2004), and/or to the date of the caterpillar peak (this study), and thus not an evolutionary response to selection. Our analyses showed that individual female Pied Flycatchers respond facultatively to the changes in the timing of food availability they experience in their life: they lay earlier when the food peak is early. The individual response of clutch size to LD was stronger in years with an early food peak, and the strength of this response was comparable with the average population-level response. The effect of temperature on the timing of the food peak, and its effect on the correlation between the life-history variables clutch size and LD, is thus rather a phenotypic response than a genotypic response to selection for a steeper relationship between clutch size and LD.

The steeper decline of clutch size in years with an early food peak is adaptive, as the fitness consequences of hatching date depend upon the timing of the food peak: in years with a late food peak, the chance that an egg results in local recruitment first increases with hatching date and later declines (Fig. 4). This means that laying an extra egg, in principle, results in a twofold advantage: more chicks are born and each chick has a higher survival chance because of the extra day it takes to lay an egg. Therefore, we should not expect the birds to reduce clutch size strongly with LD early in the season, but later they should do so. In years with an early food peak, the recruitment rate declined strongly throughout the season, and as each extra egg takes an extra day, this was probably at the expense of lower recruitment. In those circumstances we might expect the birds to reduce clutch size more rapidly throughout the season and to reduce the incubation time by starting incubation before the last egg is laid, as was found in this study.

Under favourable conditions with high food availability and/or high temperatures, incubation periods are shorter (Nilsson & Smith, 1988; Siikamaki, 1995; Sanz, 1996). Although incubation time was also shorter for females laying larger clutches (Siikamaki, 1995), experimentally enlarged clutches took longer to incubate (Moreno & Carlson, 1989; Siikamaki, 1995). This suggests that larger clutches take longer to incubate, but that females in good condition can lay larger clutches and also shorten their incubation time. Incubation periods declined during the season, and all these factors suggest that birds increased the speed of incubation under favourable circumstances, possibly because they had a higher level nest attendance (Lifjeld & Slagsvold, 1986). As our flycatchers did not fully adjust their LD to the advance of the food peak, the environmental conditions for females laying and incubation probably improved over time, because they were laying closer to the caterpillar peak, thereby resulting in a shorter incubation time. This may, in part, be because of higher nest attentiveness and more efficient incubation, and possibly also due to the fact that birds started incubating sooner relative to clutch completion and therefore allowed greater hatching asynchrony within their clutches. However, data collected in our population from a small sample of eight clutches in 2002 do not show greater hatching asynchrony as compared with other studies (hatching spread was on average 19 h; Slagsvold, 1986; Hillstrom & Olsson, 1994). This suggests that the birds did not allow greater hatching asynchrony, but rather that they reduced incubation time *per se*.

Apart from the time cost of laying eggs, the variation in date-related recruitment rates could have led to a change in the optimal clutch size with LD. Individuals are expected to choose their LD and clutch size in order to maximize their lifetime fitness, which includes both

the value of the current clutch and the future reproductive perspectives (Charnov & Krebs, 1974). Experimental brood size manipulations have shown that raising larger broods incurs a survival cost to the parent (Askenmo, 1979; Gustafsson & Sutherland, 1988), but we do not know whether this cost changes throughout the season, and whether such a seasonal pattern has changed over the years in our population. If we assume that this cost is unrelated to LD, a steeper decline in recruitment rate with date leads to a lower value of the current clutch at later dates, which shifts the balance between current and future reproduction (Daan *et al*., 1988, 1990). Thus, in the late years when recruitment rates declined most steeply with LD, parents breeding later in the season would have experienced a lower reproductive value from the current clutch. Therefore, they may have invested less and thereby enhanced their future fitness. The change in the fitness landscape with LD could thus qualitatively explain why the optimal clutch size declines more steeply in years with an early food peak.

A full understanding of how organisms evolve in response to climate change and whether the changes in different life-history traits are adaptive requires knowledge concerning how organisms interact with other levels of the food chain. By studying the effect of the timing of the caterpillar peak on reproductive decisions in Pied Flycatchers we are able to understand why these birds change both LD and clutch size. The lack of knowledge regarding the timing of food availability may have prevented a full understanding of patterns in LDs and clutch size in a similar study on Tree Swallows *Tachycineta bicolor* (Winkler *et al*., 2002). It seems paradoxical that our Pied Flycatcher population now lays larger clutches, while they do not adjust their LD appropriately to climate change. However, the increase in clutch size is mainly because of more birds laying early in the season and recruitment rates for these very early birds have increased. Meanwhile, clutch size for the declining proportion of birds laying late has declined more strongly, also reflecting the stronger decline in fitness in recent years.

Climate changes thus may alter an organism's optimal response across a suite of different life-history traits, because the covariation in selection on such life-history traits is itself affected by climatic variables. In some cases the response of an organism may be constrained by genetic correlations and become maladaptive, as one trait cannot be changed independently from another. In our case, the response of the population was in agreement with what we expected from the changing selection pressures, and individuals were flexible in changing their clutch size vs. LD relationship as environmental circumstances changed as a result of climate change.

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